

# Chapter 6A

# Plankton

(phytoplankton,  
zooplankton,  
microbes  
and viruses)

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## Keynote points

- Single-celled microbes are the most abundant and diverse form of marine life. Food webs based on them sustain most ocean biodiversity.
- Marine phytoplankton account for about 50 per cent of the Earth's primary production, oxygen supply and N<sub>2</sub>-fixation. Diatoms and picoplankton (< 2 µm) account for most marine primary production.
- Driven by upper-ocean warming, increases in the vertical separation of layers of water (stratification) and decreases in inorganic nutrient inputs to the part of the ocean where photosynthesis is possible (the euphotic zone) are likely to result in:
  - Decreases in phytoplankton productivity and cell size;
  - Increases in energy flow through microbial food webs relative to that through metazoan food webs (plankton > 20 µm);
- Decreases in the export of biological production to the deep ocean. Such decreases would reduce the capacity of the ocean to absorb CO<sub>2</sub>, accelerating global atmospheric warming;
- Decrease in biological production of higher trophic level.
- Climate-driven ocean acidification may reduce the abundance and distribution of calcareous plankton.
- Current global ocean observations do not specifically monitor plankton diversity. An international, integrated observing system of ocean life is needed as a component of the Global Earth Observing System of Systems.

## 1. Introduction

Marine plankton communities are comprised of viruses, prokaryotes (archaea and bacteria) and eukaryotes (protists and Metazoa). Prokaryotes and eukaryotes include both primary producers and heterotrophic consumers, and marine plankton represent the most phylogenetically diverse group of organisms on Earth (Colomban and others, 2015; United Nations, 2017a). The focus in the present subchapter is on plankton assemblages of the upper ocean (0 to -1,000 m) and climate-driven changes in plankton that are most likely to have an impact on ecosystem services.

Unicellular microbes account for most biomass, biodiversity and metabolic activity in the oceans (Gasol and others, 1997; Azam and

Malfatti 2007; Salazar and Sunagawa, 2017; Bar-On and others, 2018) and play critical roles in the provision of marine ecosystem services (Palumbi and others, 2009; Liqueste and others, 2013). In particular, phytoplankton account for some 50 per cent of the Earth's net primary production (NPP) that fuels marine food webs and for some 50 per cent of the Earth's oxygen supply (Field and others, 1998; Westberry and others, 2008); and planktonic food webs support most fisheries (Blanchard and others, 2012; Boyce and others, 2015), fuel the biological pump<sup>1</sup> (Honjo and others, 2014) and sustain biodiversity (Beaugrand and others, 2013; Vallina and others, 2014). Phytoplankton NPP and the flows of nutrients through planktonic food webs make significant contributions to

<sup>1</sup> Biologically mediated export of particulate organic matter and calcium carbonate to the deep ocean (below 1,000 m).

at least 14 Sustainable Development Goals (Wood and others, 2018), first of all Goal 14 (Conserve and sustainably use the oceans, seas and marine resources for sustainable development).<sup>2</sup>

The objectives of the present subchapter are to: (a) describe the current composition of plankton assemblages and past trends in their diversity and productivity at the global and regional levels; (b) summarize predicted, climate-driven trends in those plankton assemblages; and (c) identify gaps in current

knowledge. The climate-driven changes in the upper-ocean environment targeted in the present section are ocean warming and ocean acidification.<sup>3</sup> This information is particularly relevant to chapters 5 (trends in the physical and chemical state of the ocean) and 10 (changes in nutrient inputs to the marine environment). Subjects addressed in the present subchapter that were not specifically covered in chapter 6 of the first *World Ocean Assessment* (United Nations, 2017b) include past and projected trends in the diversity of plankton.

## 2. Summary of chapter 6 of the first *World Ocean Assessment*

Regional and global patterns of NPP by phytoplankton and benthic macrophytes, nutrient cycling in the upper ocean and anthropogenic impacts on those processes were studied, leading to the following findings:

- With the exception of coastal waters subject to riverine inputs of nutrients and high-nutrient low-chlorophyll zones, the global pattern of phytoplankton NPP reflects the pattern of deep-water nutrient (nitrogen and phosphorus) inputs to the euphotic zone.<sup>4</sup>
- Phytoplankton NPP in subtropical gyres decreased from 1998 to 2006 as a result of climate-driven upper-ocean warming and associated decreases in nutrient supply, while NPP has increased in coastal ecosystems as a result of increases in land-based nutrient inputs. This has led to a global spread of hypoxia in the ocean, a decline in the spatial extent of seagrass beds and increases in the occurrence of toxic phytoplankton events.
- Phytoplankton species diversity tends to be lowest in polar and subpolar waters, where fast-growing species account for most NPP, and highest in tropical and subtropical waters, where small phytoplankton (< 10 µm) account for most NPP.
- As the upper ocean warms and becomes more stratified, it is likely that small phytoplankton species will account for an increasingly large fraction of NPP, resulting in decreases in fish stocks and organic carbon export to the deep sea.
- With increases in upper-ocean temperatures at high latitudes, the spatial ranges of copepod species in the North Atlantic have expanded to higher latitudes and seasonal peaks in abundance are occurring earlier in the year for temperate species.

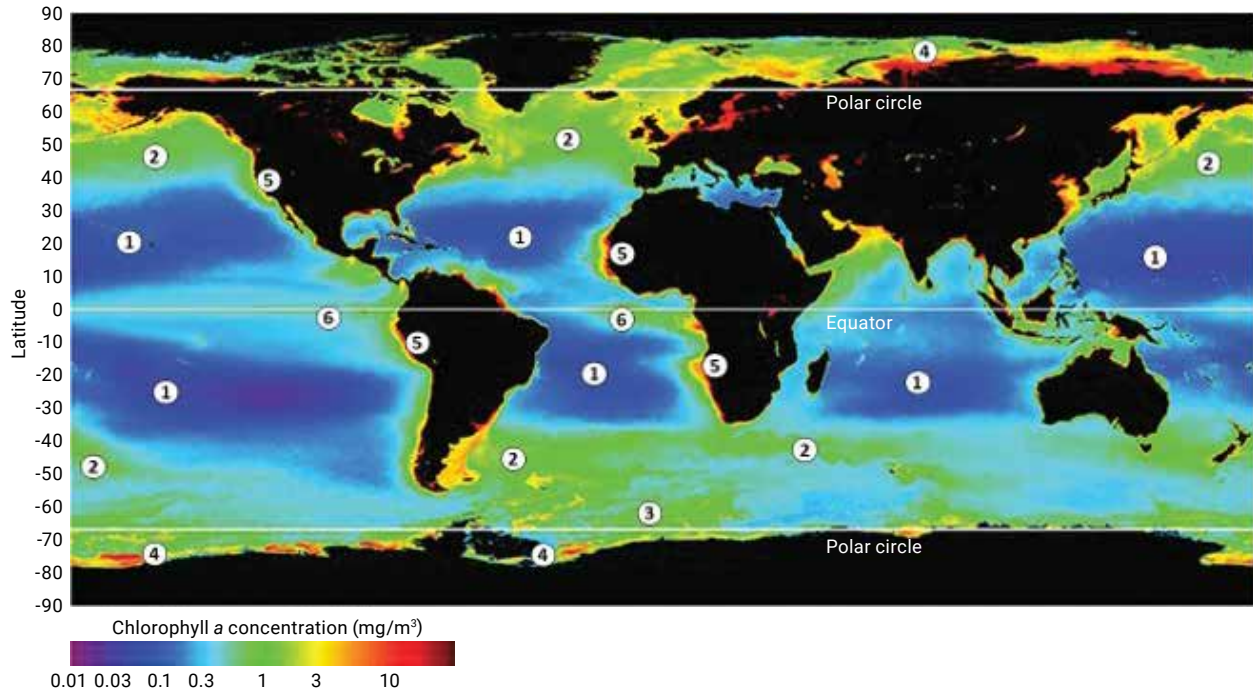
<sup>2</sup> See General Assembly resolution 70/1.

<sup>3</sup> Ocean acidification refers to a reduction in the pH of the ocean over an extended period of time, caused primarily by the uptake of CO<sub>2</sub> from the atmosphere.

<sup>4</sup> The euphotic zone is the upper layer of the ocean into which sufficient light penetrates for photosynthesis to occur.

### 3. Regions targeted in the present *World Ocean Assessment*

#### Mean sea surface chlorophyll a concentration (1997–2010) and six regions targeted in the present report



Source: adapted from Sundby and others (2016).

Note: 1, central gyres; 2, high-latitude spring bloom regions; 3, Antarctic circumpolar region; 4, polar sea ice region; 5, coastal upwelling region; and 6, equatorial upwelling region (blue:  $< 0.1 \text{ mg}/\text{m}^3$ ; green:  $0.1\text{--}1.0 \text{ mg}/\text{m}^3$ ; yellow:  $1\text{--}3 \text{ mg}/\text{m}^3$ ; and red:  $> 3 \text{ mg}/\text{m}^3$ ).

Phytoplankton NPP varies regionally (Behrenfeld and others, 2006; Uitz and others, 2010; United Nations, 2017c), and the global ocean has been subdivided into regions by the Intergovernmental Panel on Climate Change accordingly (Hoegh-Guldberg and Poloczanska, 2017). Of the seven regions defined by the Panel, those targeted in the present section represent high- and low-latitude systems, systems in which the primary input of nutrients is from deep water through vertical mixing or upwelling and systems that exhibit a broad range of trophic states<sup>5</sup> (that do not reflect land-based inputs of nutrients). The six targeted

regions (as numbered in the figure above) are as follows:

1. The five subtropical central gyres, the largest biomes of the upper ocean (about 40 per cent of the surface of the ocean, 22 per cent of the annual NPP of the ocean);
2. High-latitude spring bloom regions (about 25 per cent of the surface of the ocean, 43 per cent of the annual NPP of the ocean);
3. Antarctic circumpolar region of the Southern Ocean (about 12 per cent of the surface of the ocean, about 9 per cent of the annual NPP of the ocean);

<sup>5</sup> From oligotrophic regions with low mean annual chlorophyll a concentrations ( $< 0.1 \text{ mg m}^{-3}$ ) to eutrophic regions with relatively high mean concentrations ( $1\text{--}30 \text{ mg m}^{-3}$ ).

4. Polar sea ice regions of the Arctic Ocean and Southern Ocean (about 4 per cent of the surface of the ocean, 1–2 per cent of annual NPP of the ocean);
  5. Coastal upwelling regions (about 2 per cent of the surface of the ocean, 7 per cent of the annual NPP of the ocean);
  6. Equatorial upwelling regions (about 8 per cent of the surface of the ocean, 9 per cent of the annual NPP of the ocean).
- Collectively, those six regions encompass 90 per cent of the surface of the ocean and account for 90 per cent of the NPP of the ocean.

## 4. Estimating plankton diversity

### 4.1. Species diversity

Accurate estimates of plankton species diversity at the regional and global levels based on the microscopic examination of ocean samples are not possible at the present time, owing to severe undersampling<sup>6</sup> (Appeltans and others, 2012), the rapidly growing number of cryptic species<sup>7</sup> revealed by metagenomics (Delong, 2009; Goetze, 2010; Lindeque and others, 2013; Harvey and others, 2017), larval stages of zooplankton that lack clear diagnostic characteristics (Bucklin and others, 2016) and a lack of consensus among microbiologists on the definition of species (Amaral-Zettler and others, 2010). The problem of undersampling can only be addressed by increasing the time-space resolution of sampling. In this regard, the importance of expanding and sustaining support for the Global Alliance of Continuous Plankton Recorder Surveys (Batten and others, 2019) and for the development of an integrated ocean life observing system (Canonica and others, 2019) must be stressed.

### 4.2. Functional diversity

Grouping organisms into functional groups that share common characteristics (size and ecological roles) can be more useful ecologically than taxonomic groupings (Litchman and others, 2010; Mitra and others, 2016). The size spectrum of plankton spans over seven orders of magnitude (Boyce and others, 2015; Sommer and others, 2017) and is reflected in the pathways by which phytoplankton NPP is recycled in the upper ocean, channelled to fisheries or exported to the interior of the ocean through the biological pump (Ward and others, 2012; Acevedo-Trejos and others, 2018). Plankton have been categorized by size into picoplankton (0.2–2 µm), nanoplankton (2–20 µm), microplankton (20–200 µm), mesoplankton (200 µm to 20 mm), macroplankton (20–200 mm) and megaplankton (> 200 mm) (Sieburth and others, 1978; Sommer and others, 2017). At the level of the major ocean basins, phytoplankton biomass and the fraction of large phytoplankton generally increase as the availability of dissolved inorganic nutrients increase, a pattern that reflects the importance of nutrient supplies as a parameter of phytoplankton NPP and community composition (Mousing and others, 2018).

<sup>6</sup> Measurements are too sparse in time and space to estimate plankton biodiversity accurately at the regional and global levels.

<sup>7</sup> Genetically distinct species (based on operational taxonomic units) that do not exhibit clear morphological differences. Such units are used to estimate species richness on the basis of genetic differences (Caron and others, 2009).

From a functional perspective, marine food webs can be divided into two categories based on size (Fenchel, 1988; Pomeroy and others, 2007):

- (a) Microbial food webs populated by pico-phytoplankton and nanophytoplankton, heterotrophic bacteria and protozoan consumers that are fuelled primarily by pico-phytoplankton NPP (including the release of dissolved organic matter by primary producers and consumers);
- (b) Metazoan food webs populated by micro-phytoplankton and metazoan plankton that

are fuelled primarily by microphytoplankton productivity and microbial food webs.

Microbial food webs account for most living biomass and nutrient recycling in the ocean (Del Giorgio and Duarte 2002; Sunagawa and others, 2015), while metazoan food webs support most fisheries and the biological pump (Legendre and Michaud, 1998; Sommer and others, 2002). Thus, changes in the balance between those two food webs are likely to have major impacts on the provision of ecosystem services (Müren and others, 2005; Worm and others, 2006; Sommer and others, 2016).

## 5. Microbial plankton

### 5.1. Phytoplankton

Major taxa in terms of their contribution to global NPP include prokaryotic cyanobacteria and eukaryotic diatoms, coccolithophores and chlorophytes (Not and others, 2007; Simon and others, 2009; Uitz and others, 2010; Flombaum and others, 2013).

#### 5.1.1. Diversity and functional groups of phytoplankton

Five functional groups of phytoplankton have been recognized on the basis of their size and roles in pelagic food webs and nutrient cycles (Chisholm, 1992; Le Quéré and others, 2005; Marañón and others, 2012): photosynthetic picoplankton, silicifying microplankton, calcifying nanoplankton, nitrogen-fixing mesoplankton and dimethyl sulphide-producing nanoplankton. For the purposes of the present subchapter, toxic microplankton have been added to this list. Changes in the relative abundance, productivity and toxicity of those functional groups have major repercussions on their capacity to support ecosystem services.

#### 5.1.1.1. Picoplankton

Picoplankton include two genera of cyanobacteria (*Prochlorococcus* and *Synechococcus*) and a diverse ensemble of picoeukaryotes from several phyla (Not and others, 2007; Kirkham and others, 2013). They are globally ubiquitous, account for some 50 per cent of the NPP of the ocean (Agusti and others, 2019) and fuel microbial food webs (Marañón and others, 2001, 2015). It is estimated that *Prochlorococcus* accounts for 17–39 per cent of picoplankton biomass globally, *Synechococcus* for 12–15 per cent and picoeukaryotes for 49–62 per cent (Buitenhuis and others, 2012). *Prochlorococcus* dominates the phytoplankton in warm (> 15 °C), nutrient-poor waters (Chisholm, 2017). *Synechococcus* has a broader, more uniform distribution and is more abundant than *Prochlorococcus* under cooler, nutrient-rich conditions (Follows and others, 2007; Flombaum and others, 2013). Picoeukaryotes tend to increase in abundance with increasing nutrient levels, often dominating the phytoplankton at high-latitudes (Li, 1994; Worden and Not, 2008; Kirkham and others, 2013). Those organisms exhibit extraordinary genomic diversity that underlies their broad geographical distribution (Vaulot, 2008; Kent and others, 2016).

#### 5.1.1.2. Silicifying microplankton: diatoms

Diatoms dominate microphytoplankton in cold, turbulent, nutrient-rich waters (Malone, 1980; Rousseaux and Gregg, 2015). They account for 40–50 per cent of global marine NPP, fuel metazoan food webs and account for some 40 per cent of carbon export through the biological pump (Honjo and others, 2014; Tréguer and others, 2018). Diatoms are therefore important players in the global carbon cycle.

#### 5.1.1.3. Calcifying nanoplankton<sup>8</sup>

Coccolithophores (dominated by *Emiliana huxleyi*) are globally ubiquitous, function as both a sink (photosynthesis) and a source (calcification) of CO<sub>2</sub> and are therefore important players in the global carbon cycle (Sarmiento and others, 2002; Balch and others, 2016). *E. huxleyi* forms the “great calcite belt” that surrounds Antarctica between the subantarctic and polar fronts (Balch and others, 2016; Nissen and others, 2018). There is evidence that *E. huxleyi* produces more biogenic CaCO<sub>3</sub> than any other organism on Earth (Iglesias-Rodríguez and others, 2002). Blooms tend to occur following seasonal diatom blooms (Brown and Yoder, 1994; Smith and others, 2017). *E. huxleyi* harbours a pan-genome of extensive genetic variability that underpins its cosmopolitan distribution and its capacity to bloom under a wide variety of environmental conditions (Read and others, 2013).

#### 5.1.1.4. Nitrogen-fixing mesoplankton<sup>9</sup>

Planktonic cyanobacteria account for about half of the Earth’s N<sub>2</sub>-fixation (Karl and others, 2002; Landolfi and others, 2018) and are the largest source of fixed nitrogen in the

global ocean (Galloway and others, 2004; Gruber, 2004). The group includes unicellular symbionts (diatom-diazotroph associations) and colonial genera (e.g., *Trichodesmium*) (Delmont and others, 2018; White and others, 2018). Most marine nitrogen fixation occurs in the subtropical gyres (Gruber, 2019) where *Trichodesmium* is most abundant at temperatures above 20°C (Breitbart and others, 2007; Monteiro and others, 2010).

#### 5.1.1.5. Dimethylsulphoniopropionate-producing nanoplankton<sup>10</sup>

Over 90 per cent of dimethyl sulphide emissions to the atmosphere come from dimethylsulphoniopropionate produced in the ocean, most of which by Prymnesiophyceae (e.g., *Phaeocystis* spp. and *Emiliana huxleyi*) and Dinophyceae (e.g., *Prorocentrum minimum*) during blooms (Keller and others, 1989; Bullock and others, 2017). *Phaeocystis* is a cosmopolitan genus with a life cycle that alternates between free-living nanoplankton (3–9 µm) and large (> 2 mm) gelatinous colonies (Schoemann and others, 2005). The latter develop during massive summer blooms in high-latitude spring bloom regions and during summer blooms in polar sea ice regions and in the Antarctic circumpolar region (Schoemann and others, 2005; Vogt and others, 2012). Blooms of *Prorocentrum minimum* occur in regions with relatively high anthropogenic nutrient inputs, and its global distribution is expected to expand, given that anthropogenic nutrient inputs are projected to more than double by 2050, unless inputs are controlled more effectively on a global scale (Glibert and others, 2008).

<sup>8</sup> Calcifying plankton include taxa that create shells, skeletons or other structures from calcium carbonate. This is a taxonomically diverse group that includes phytoplankton such as coccolithophores, zooplankton such as pteropods and the larval stages of benthic bivalve molluscs and echinoderms.

<sup>9</sup> Nitrogen fixation is not limited to mesozooplankton. There is evidence that there are non-cyanobacterial diazotrophs (bacteria and archaea) in the oceans (Benavides and others, 2018).

<sup>10</sup> Dimethylsulphoniopropionate is the biogenic precursor of dimethyl sulphide, which represents a large source of sulfur going into the Earth’s atmosphere, where it helps to drive the formation of clouds that block solar radiation from reaching the Earth’s surface and reflect it back into space.

#### 5.1.1.6. Toxin-producing microplankton

Among the 5,000 species of extant marine phytoplankton (Sournia and others, 1991), some 80 or so species have the capacity to produce potent toxins that find their way through fish and shellfish into humans (Hallegraeff and others, 2004). Most toxic species are dinoflagellates that cause paralytic shellfish poisoning (e.g., *Alexandrium* spp.), diarrhoeic shellfish poisoning (e.g., *Dinophysis* spp.), neurotoxic shellfish poisoning (e.g., *Karenia* spp.), azaspiracid shellfish poisoning (e.g., *Protoperdinium crassipes*) and ciguatera fish poisoning (e.g., *Gambierdiscus toxicus*). One diatom genus (*Pseudo-nitzschia* spp.) also causes amnesic shellfish poisoning (Lelong and others, 2012). Toxin-producing microplankton have a cosmopolitan distribution (Hallegraeff and others, 2004).

### 5.2. Protozoan consumers

Most heterotrophic protozoa fall into the nano- and micro-zooplankton size classes and are major consumers in microbial food webs and important links to metazoan food webs (Landry and Calbet, 2004; Mitra and others, 2016). Their diversity can be described in terms of three basic body plans that broadly determine their ecological roles: amoeboid, flagellated and ciliated forms (Fuhrman and Caron, 2016).

Amoeboid foraminifers are most abundant in high-latitude spring bloom regions and least abundant in subtropical gyres (Berger, 1969). They are major producers of marine calcareous shells deposited on the ocean floor (Schiebel and Hemleben, 2005). Radiolaria are common in the euphotic zone in tropical and subtropical oceanic regions globally and much less abundant in coastal upwelling, high-latitude spring bloom and polar regions (Caron and Swanberg, 1990).

Heterotrophic nanoflagellates are the most abundant protozoan consumers and control the abundance of bacterioplankton (Fenchel, 1982; Massana and Jürgens, 2003). While nanoflagellates are important grazers of picophytoplankton in oligotrophic habitats, heterotrophic microflagellates (e.g., dinoflagellates) can be important consumers of microphytoplankton, including bloom-forming diatoms (Sherr and Sherr, 2007; Calbet, 2008).

Microzooplankton (dinoflagellates and ciliates) have been estimated to graze over half of daily global phytoplankton NPP and exert significant top-down control on phytoplankton blooms in ecosystems from the Southern Ocean (Swailethorp and others, 2019) and the western Arctic Ocean (Sherr and others, 2009) to temperate coastal ecosystems (Pierce and Turner, 1992).

### 5.3. Heterotrophic bacteria and archaea

Bacterial assemblages are typically dominated by a small number of phylotypes<sup>11</sup> (Yooseph and others, 2010), the 20 most abundant of which fall into one of four groups (Amaral-Zettler and others, 2010; Luo and Moran, 2014):  $\alpha$ -Proteobacteria (SAR11, Rhodobacteraceae),  $\gamma$ -Proteobacteria (SAR86), Bacteroidetes (Flavobacteriaceae) and Actinobacteria, most abundant of which are  $\alpha$ -Proteobacteria (Lefort and Gasol, 2013; Giovannoni, 2017). Species richness tends to decrease toward the poles for both the animal and plant kingdoms (Wietz and others, 2010).

Four major groups of archaea (marine groups I–IV) are abundant in the ocean (Church and others, 2003; Danovaro and others, 2017). Marine group I archaea are among the most abundant and widely distributed, from polar to tropical waters (Karner and others, 2001;

<sup>11</sup> A group of genetically similar organisms that may be grouped at different taxonomic levels, such as species, family, class or phylum.

Santoro and others, 2019). Although bacteria tend to outnumber archaea, the latter make an important contribution to microbial biomass in deep waters (Danovaro and others, 2015).

## 5.4. Viruses

Viruses play important roles in marine food webs and nutrient recycling via their control of the abundance of microbial populations and the release of dissolved organic matter by cell lysis (Rohwer and Thurber, 2009; Sieradzki and others, 2019). Viruses, including free-living virions, are the most abundant biological entities in the oceans and are a major

reservoir of genetic diversity (Suttle, 2007; Simmonds and others, 2017). The majority of viruses are bacteriophages (Coutinho and others, 2017), and their abundance is correlated with the abundance of bacteria from regional to global scales (Fuhrman and Caron, 2016). Metagenomic analyses indicate that there are thousands of different virions in a few litres, with the most abundant genotypes represented by a relatively small fraction of the entire assemblage (Breitbart and others, 2004; Angly and others, 2006). However, despite recent advancements in metagenomics such as those, it is clear that this is the “tip of the iceberg” in terms of viral biodiversity (Paez-Espino and others, 2019).

# 6. Metazoan zooplankton

## 6.1. Holoplankton<sup>12</sup>

Metazoan holoplankton have been described from 15 phyla (Bucklin and others, 2010; Wiebe and others, 2010). As a group, they exhibit diverse feeding types (Kiørboe, 2011), from filter-feeders (e.g., copepods, euphausiids and tunicates) to passive ambush predators (e.g., ctenophores and some pteropods) and active ambush predators (e.g., chaetognaths and some amphipods). Like other groups of animals, the diversity of holozooplankton tends to decrease toward the poles (Lindley and Batten, 2002; Burridge and others, 2017). Diversity also tends to be higher when biomass is low (e.g., subtropical gyres) and lower when biomass is high (e.g., coastal upwelling and high-latitude spring bloom regions) (United Nations, 2017a).

### 6.1.1. Crustaceans

About half of the known species of holoplankton are crustaceans (Verity and Smetacek,

1996; United Nations, 2017a). Copepods are by far the most abundant and are a key trophic link between phytoplankton and fisheries (e.g., Möllmann and others, 2003; Beaugrand, 2005). While copepod abundance is generally highest in regions where high NPP occurs seasonally, biodiversity is generally highest in warm water regions where NPP is relatively low (Rombouts and others, 2009; Valdés and others, 2017).

With nearly 100 documented species (Baker and others, 1990), euphausiids (krill) occur throughout the global ocean and, like copepods, are most abundant during periods of high phytoplankton productivity (Baker and others, 1990). They are especially abundant in the Southern Ocean, where they play a crucial role in the food web and are a target for fisheries (Mangel and Nicol, 2000; Boopendranath, 2013).

There are approximately 200 described species of planktonic ostracods (Angel and others, 2007) and approximately 300 species

<sup>12</sup> Species that live their entire life cycles as plankton.

of hyperiid amphipods<sup>13</sup> (Vinogradov, 1996; Boltovskoy and others, 2003). Ostracod species richness tends to be highest in the mesopelagic zone at low latitudes (< 50°N) and in the epipelagic zone at higher latitudes. The majority of hyperiids spend at least part of their life cycle living as commensals of salps, jellyfish, ctenophores or siphonophores (Madin and Harbison, 1977; Gasca and Haddock, 2004), and their species richness is highest in regions where gelatinous zooplankton are most abundant.

### 6.1.2. Gelatinous zooplankton

This diverse group includes cnidarians (jellyfish),<sup>14</sup> ctenophores (comb jellies), chaetognaths (arrow worms), tunicates (salps, doliolids and appendicularians) and molluscs (pteropods and heteropods) (Alldredge, 1984; Jennings and others, 2010). As a group, tunicates are well adapted to life in oligotrophic oceans, where their diversity and abundance are often greater than those of planktonic crustaceans (Alldredge and Madin, 1982; Madin and Harbison, 2001). Species richness is highest in jellyfish (more than 1,000 species)

(Purcell and others, 2007; Pitt and others, 2018), followed by molluscs (250 species) (Jennings and others, 2010), ctenophores (200 species) (Harbison, 1985; Madin and Harbison, 2001), tunicates (145 species) (Deibel and Lowen, 2012) and chaetognaths (100 species) (Daponte and others, 2004).

## 6.2. Meroplankton

Meroplankton are larval stages of benthic and pelagic adults (e.g., shellfish and fish) and are, therefore, temporary members of the plankton. Their contribution to plankton diversity occurs episodically or seasonally, and their abundance relative to holoplankton decreases with increasing depth and increasing latitude (Silberberger and others, 2016; Costello and Chaudhary, 2017). The distribution, diversity and fecundity of adults that have a planktonic larval stage are inextricably linked to the abundance and diversity of their meroplanktonic larvae which, in turn, influence the distribution and diversity of their adult stage (Miron and others, 1995; Hughes and others, 2000).

# 7. Documented trends

## 7.1. Global

The study of satellite time series (1998–2015) of sea surface chlorophyll *a* has not yet revealed a long-term trend in NPP on a global scale (Gregg and others, 2017). However, microplankton diatom biomass has declined relative to picophytoplankton in most regions during the period under review (Rousseaux and

Gregg, 2015; Gregg and others, 2017), a trend that appears to be related to upper-ocean warming, increases in vertical stratification<sup>15</sup>, and decreases in nutrient supplies from the deep sea (Daufresne and others, 2009; Basu and Mackey, 2018).

A comparison of known toxic events in 1970 with those observed in 2017<sup>16</sup> suggests that

<sup>13</sup> An order of amphipods that is exclusively marine.

<sup>14</sup> Although jellyfish have a life cycle with a benthic polyp stage and a planktonic medusa stage, they are considered to be holoplankton because the sexually reproducing stage (medusa) is planktonic.

<sup>15</sup> A water column becomes vertically stratified when a less dense body of water develops (owing to an increase in temperature, a decrease in salinity, or both) over deeper, denser water. This process limits mixing between the surface mixed layer and the deep ocean.

<sup>16</sup> United States National Office for Harmful Algal Blooms, "Distribution of HABs throughout the World". Available at [www.whoi.edu/website/redtide/regions/world-distribution](http://www.whoi.edu/website/redtide/regions/world-distribution).

the public health and economic impacts of toxic events have increased in frequency and have spread globally (Hallegraeff and others, 2004):

- Paralytic shellfish poisoning events caused by *Alexandrium tamarense* and *A. catenella* increased from 19 coastal sites (including 12 in North America and 4 in western Europe) to 118 coastal sites (including 26 in North America, 25 in western Europe, 36 in the western Pacific, 9 in Australia and New Zealand, 7 in South America, 7 in Africa and 4 in India).
- Diarrhoeic shellfish poisoning events caused by *Dinophysis* spp. increased from 15 coastal sites (including 13 in western Europe) to 71 coastal sites (8 in North America, 37 in western Europe, 9 in South America, 7 in Australia and New Zealand, 6 in Japan and 4 in India).
- Amnesic shellfish poisoning events caused by *Pseudo-nitzschia* spp. increased from 1 coastal site, in North America, to 31 coastal sites (including 12 in North America, 9 in western Europe and 9 in Australia and New Zealand).

While there is reason to suspect that the combined effects of increases in coastal eutrophication, sea surface temperature and vertical stratification may favour the growth of dinoflagellates, the underlying causes of those trends remain a matter of speculation (Wells and others, 2015).

Upper-ocean warming is influencing the biogeography and phenology of plankton species (Hays and others, 2005; Thackeray and others, 2010; Mackas and others, 2012). On average, seasonal spring peaks in biomass have advanced by 4.4 days per decade, with a standard error of 0.7 days, and the leading edges of species distributions have extended polewards by 72 km per decade (1920–2010), with a standard error of 0.35 km (Hoegh-Guldberg

and others, 2014). While holoplankton show large shifts in both biogeography and phenology in response to upper-ocean warming, meroplankton show relatively small shifts in distribution but greater changes in phenology (Edwards and Richardson, 2004), changes that are likely to have feedback effects on the abundance of adult populations.

## 7.2. Polar sea ice regions

### 7.2.1. Southern Ocean

A significant interannual trend in NPP in the Southern Ocean as a whole has not been documented (Arrigo and others, 2008). However, opposing trends in NPP in the Ross Sea (increasing) and the West Antarctic Peninsula (decreasing) coincided with increases (Ross Sea) and decreases (West Antarctic Peninsula) in sea ice extent<sup>17</sup> (Montes-Hugo and others, 2009; Ducklow and others, 2013). The decrease in NPP was associated with a shift in the size spectrum of phytoplankton from microplankton-dominated (diatoms) assemblages to nanoplankton and picoeukaryotes as sea surface temperature increased (Moline and others, 2004; Montes-Hugo and others, 2009). Warming and the shift to smaller phytoplankton have also been associated with a range extension of *Emiliania huxleyi* from the Antarctic circumpolar region into the polar sea ice region (Cubillos and others, 2007).

Inter-annual variations in the extent of sea ice off the Antarctic Peninsula also appear to be reflected in the relative abundance of two dominant grazers: krill (*Euphausia superba*) and salps (*Salpa thompsoni*). Krill recruitment, which depends on the survival of larval krill during winter, is the population parameter most likely to be altered by climate change (Flores and others, 2012). *E. superba* has been found to be more abundant following winters with extensive sea ice cover, while salps have been

<sup>17</sup> See Michon Scott and Kathryn Hansen, "Sea ice", NASA Earth Observatory, 16 September 2016.

more abundant following winters when the spatial extent of sea ice is relatively low (Loeb and others, 1997). Thus, while krill populations may have suffered from sea ice decline, salps appear to have benefited from warming surface waters during the twentieth century (Loeb and Santora 2012). The observed decrease in sea ice extent portends a long-term shift from a food web dominated by *E. superba* to one dominated by salps, with unknown cascading effects on the abundance of vertebrate predators (Henschke and others, 2016).

### 7.2.2. Arctic Ocean

The Arctic Ocean is in the process of transitioning to a warmer state (cf., Buchholz and others, 2010). Unlike the Antarctic, sea ice extent has decreased (1998–2015) in all sectors of the Arctic, owing to increases in sea surface temperature (Kahru and others, 2016), a trend that is associated with increases in NPP (Arrigo and van Dijken, 2011; Hill and others, 2017) and increases in the biomass of picoeukaryotes at the expense of microplankton diatoms as the vertical stratification of the water column increased (Li and others, 2009).

As in coastal waters of the West Antarctic Peninsula, krill are an important prey for a number of species, including smelt. From 1984 to 1992 and from 2007 to 2015, krill abundance increased in the south-western and central Barents Sea, despite high smelt predation, probably as a result of increasing temperatures, stronger advection of krill into the Barents Sea (Slagstad and others, 2011) and increases in phytoplankton NPP (Dalpadado and others, 2014). Warming has also influenced the relative abundance of krill species, with the boreal species *Meganycitiphanes*

*norvegica* increasing and the cold water species *Thysanoessa raschii* decreasing (Rasmussen, 2018).

## 7.3. North Atlantic high-latitude spring bloom region

In the seasonally nutrient-rich waters of the North Atlantic high-latitude spring bloom region, upper-ocean warming and an earlier set-up of the seasonal pycnocline<sup>18</sup> combine to increase the length of the growing season and the availability of sunlight. As a result, NPP has been increasing in recent decades (1979–2010) (Dalpadado and others, 2014; Raitos and others, 2014), a trend that has been accompanied by increases in picoeukaryotes and coccolithophores relative to diatoms (Li and others, 2009), a reduction in the average size of phytoplankton and zooplankton and an increase in the biodiversity of plankton assemblages (Hoegh-Guldberg and Bruno, 2010; Edwards and others, 2013).

Poleward expansions in the range of plankton species in response to upper-ocean warming have been well documented (Poloczanska and others, 2013), especially in the North Atlantic: *Emiliana huxleyi* into the Barents Sea (Smyth and others, 2004); *Calanus helgolandicus* replacing *C. finmarchicus* in the North Sea (Edwards and others, 2013); and a poleward expansion of the ranges of calcifying species of plankton (foraminifers, coccolithophores and pteropods) (Beaugrand and others, 2013; Winter and others, 2014).

The phenologies<sup>19</sup> of phytoplankton and zooplankton species are also changing in response to upper-ocean warming (1958–2002). For example, during the period from 1958 to

<sup>18</sup> A pycnocline is a vertical zone over which an increase in density separates a surface layer of relatively low density from a deeper layer of relatively high density. A seasonal pycnocline begins to form in the North Atlantic high-latitude spring bloom region when solar heating begins to warm the surface layer during late winter-early spring, a process that increases the availability of solar energy for photosynthesis.

<sup>19</sup> Phenology refer to the timing of biological events in plant and animal lives (e.g., reproduction and migration) in relation to changes in season and climate.

2002, the seasonal abundance of the copepod *Calanus finmarchicus* in the North Atlantic began to peak earlier, so that, by the turn of the century, abundance was peaking some 10 days earlier in the year than previously, while its food (microplankton diatoms and dinoflagellates) peaked some 30 days earlier (Edwards and Richardson, 2004). Similarly, diatom blooms in the North Sea are occurring earlier in the year than the peak in abundance of their macrozooplankton grazers (Hays and others, 2005). Such uncoupling of trophic levels has also been documented in the Baltic Sea, where the duration of the growing season during the period from 1988 to 2017 increased at a rate of 4.5 days per year, resulting in an earlier spring bloom, a prolongation of the summer biomass minimum and a later and more prolonged autumn bloom (Wasmund and others, 2019).

#### 7.4. Upwelling regions

Diatom production has been increasing (1996–2011) in eastern boundary upwelling systems (Kahru and others, 2012), while NPP increased in Pacific equatorial upwelling (Chavez and others, 2011), apparently owing to increases in upwelling (Tim and others, 2016). However, ocean acidification in coastal upwelling systems is proving to be corrosive to pteropod shells (*Limacina helicina*) (Bednaršek and others, 2014). As the habitat suitability for pteropods declines, metazoan food webs are likely to be affected (Bednaršek and others,

2012; Lischka and others, 2011), and ocean acidification is likely to have a similar impact in the Southern Ocean and the Arctic Ocean (Comeau and others, 2009; Negrete-García and others, 2019).

#### 7.5. Subtropical gyres

Owing largely to declines in diatoms and chlorophytes (Gregg and others, 2017), a significant downward trend in chlorophyll *a* (1998–2013) has been documented in all gyres, except in the South Pacific (Signorini and others, 2015). Rates of decline were greatest in the northern hemisphere and lowest in the South Atlantic Ocean and the Indian Ocean, trends that correspond to expansions of the gyres in the Atlantic Ocean and the North Pacific Ocean (Polovina and others, 2008).

Downward trends in NPP were observed in all five gyres that coincided with upper-ocean warming and decreases in phytoplankton cell size (Polovina and Woodworth, 2012). The latter is consistent with observed increases in the relative abundance of *Prochlorococcus* and *Synechococcus* (Flombaum and others, 2013; Agusti and others, 2019), trends that most likely reflect both warming temperatures (Daufresne and others, 2009; Morán and others, 2010) and decreasing nutrient supplies as the euphotic zone becomes more isolated from nutrient-rich deep water (Marañón and others, 2015; Sommer and others, 2016).

## 8. Outlook

Climate change during the course of the twenty-first century is expected to continue to drive changes in the upper ocean that have an impact on the diversity and productivity of plankton assemblages on the regional to global scales. These changes include an expansion of the subtropical gyres (Polovina and others, 2011),

ocean warming and acidification, decreases in salinity, increases in vertical stratification and decreases in inorganic nutrient supplies to the euphotic zone in the open ocean (Bopp and others, 2013). Predicted biological responses to those changes on a global scale include the following:

- (a) NPP is likely to decrease and the relative abundance of picophytoplankton is likely to increase (Daufresne and others, 2009; Morán and others, 2010) at the expense of microplankton diatoms (Bopp and others, 2005; Moore and others, 2018);
  - (b) These trends are likely to propagate through food webs resulting in decreases in the ocean's carrying capacity for fisheries (Worm and others, 2006; Chust and others, 2014) and in its capacity to sequester carbon through the biological pump (Boyd, 2015);
  - (c) The expansion of the subtropical gyres may promote increases in N<sub>2</sub> fixation (Boatman and others, 2017; Follett and others, 2018), a trend that could further perturb the global nitrogen cycle (Jiang and others, 2018);
  - (d) Plankton food webs in the polar oceans and coastal upwelling regions will be the most affected by ocean acidification, owing to the high solubility of CO<sub>2</sub> in cold waters (Bednaršek and others, 2014; Gardner and others, 2018).
- and others, 2009; Kahru and others, 2011; Dalpadado and others, 2014);
- (b) Increases in NPP, export production and the abundance of diatoms during the first half of the century in the polar sea ice region of Antarctica (Bopp and others, 2001; Kaufman and others, 2017; Moore and others, 2018);
  - (c) Expansion of the range of *Emiliania huxleyi* into the polar oceans (Winter and others, 2014) and increases in the frequency of coccolithophore blooms in high-latitude spring bloom regions (Bopp and others, 2013; Rivero-Calle and others, 2015);
  - (d) An increase in NPP and a decrease in the relative abundance of diatoms in the North Atlantic high-latitude bloom region (Bopp and others, 2005, 2013; Sundby and others, 2016).

Regional exceptions during the course of the twenty-first century are predicted to occur polewards of the subtropical gyres as a result of environmental changes in the euphotic zone, including increases in the availability of sunlight as the surface mixed layer shoals in nutrient-rich environments (promoting increases in NPP), increases in temperature and decreases in salinity (favouring the growth of small phytoplankton) (Tréguer and others, 2018). Notable examples include:

- (a) An increase in NPP and a decrease in phytoplankton size in the Arctic Ocean (Mueter

Projections of future trends in NPP in coastal upwelling regions are less certain, owing to uncertainty concerning how interactions between increases in upwelling-favourable winds (increases in upwelling, NPP and the relative abundance of diatoms) and upper-ocean warming (decreases in upwelling, NPP and the relative abundance of diatoms) will play out (Chavez and others, 2011; García-Reyes and others, 2015).

In this context, it must be emphasized that the present analysis of the impacts of climate change on plankton communities does not consider transgenerational adaptation to climate-driven changes in the upper-ocean environment (e.g., Schlüter and others, 2014; Thor and Dupont, 2015).

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